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Physiological responses of cotton to a single waterlogging at high and low N-levels

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Abstract
Surface-irrigated cotton (*Gossypium hirsutum* L.) grown on slowly draining clay soil is subjected to short-term periods of waterlogging at each irrigation which generally results in reduced productivity. The sequence of above- and below-ground plant responses to transient waterlogging and the role of N availability in modifying the immediate responses were studied. Lysimeters of Marah clay loam (a Natrustalf) were instrumented to monitor soil and plant responses to a 7-day waterlogging event beginning 67 days after sowing. Cotton ('Deltapine 61') plants (8 per lysimeter) were grown with two levels of added N (300 kg ha^{-1} and 30 kg ha^{-1}) and two irrigation treatments (flooded and control). Measured soil-O_2 levels decreased rapidly upon surface flooding because water displaced air and root zone respiration consumed O_2. The rate of O_2 consumption was 2.7 times greater in the high-N treatment than the low-N treatment. This difference was associated with a 1.8 fold difference in numbers of observed roots. Root growth was only slightly affected by flooding. Leaf growth decreased by 28%, foliage temperature increased 2.3% and apparent photosynthesis decreased by 16%. It is suggested that flooding reduced photosynthetic activity within 2 days while other stress symptoms became apparent after about 6 days. Although this stress was reflected in a trend for decreased plant productivity, the effect of flooding on boll dry mass at harvest was not significant at the level of replication used. The single waterlogging did not cause yield reductions comparable to those observed elsewhere when several waterlogging events were imposed.

Introduction

Many irrigated areas of south eastern Australia have fine textured soils with slow internal drainage. These soils, when flood irrigated, expose crops (such as cotton, *Gossypium hirsutum* L.) to a period of waterlogging during and for some time after irrigation (Mason *et al.*, 1984). Cotton subjected to waterlogging usually has reduced yield (de Bruyn, 1982; Hodgson and Chan, 1982) with the decrease being proportional to the time of inundation (up to 32 h) at each irrigation (Hodgson, 1982). Reductions in yield are probably related to slowed root growth associated with reductions in soil O_2 concentration (Huck, 1970; Patrick *et al.*, 1973). The importance of an adequately aerated root zone is indicated by the strong relation between yield and an index using air filled porosity (Hodgson, 1982) and by the results of Meek *et al.* (1980) who found reduced cotton seed yield when the water-table was less than 0.9 m below the soil surface.

Decreases in soil O_2 accompanying flooding also affect root functions such as N uptake. Constable and Hearn (1981) noted the coincidence of visual symptoms of waterlogging, reduced rates of N uptake and reduced lint yield. Decreased N uptake during waterlogging has been observed for barley

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(*Hordeum vulgare* L.) (Drew and Sisworo, 1979) and apparently can be partially overcome by N-fertilizer additions to a portion of the root zone which has adequate aeration (Drew *et al.*, 1979) or, in the case of cotton, through foliar applications of N (Hodgson, 1982).

Cotton susceptibility to waterlogging may be due to lowered soil O_2 or to reduced availability and uptake of N. The two effects may interact. While most studies have been concerned with a particular aspect of cotton response to a series of waterloggings, none have simultaneously monitored above and below ground responses in-situ during and following a single waterlogging. This paper describes an experiment in which cotton response to a single waterlogging event was monitored with the aim of establishing the sequence of response and examining the possible N-soil O_2 interaction.

Materials and methods

The experiment was conducted in a lysimeter facility (Meyer *et al.*, 1985) at the CSIRO Center for Irrigation Research, Griffith, N.S.W., Australia. The lysimeters consisted of undisturbed cores of soil (0.75 m diameter by 1.35 m deep) in steel cylinders. The soil was Marah clay loam, a Natrustalf, which when cultivated takes on vertic (cracking) characteristics. Details of the site and method of collection are given by Meyer *et al.* (1985) while additional soil profile characteristics are given by Loveday (1974). Briefly, the soil is a deep, moderately cracking clay (45–60% clay) with a bulk density of 1.5–1.6 mg mm^{-3} which, when wet, has surface infiltration rates of less than 1 mm day^{-1}. The experimental design using 8 lysimeters was completely randomised, with 2 levels of irrigation management (flooded and control), 2 levels of applied N fertilizer (high N and low N) and 2 replications. Subsequent statistical analysis of results was based on analysis of variance completely randomised design with two treatments each with two levels and two replications.

Cotton seeds ('Deltapine 61') were sown on 16 December 1982 to establish eight evenly spaced plants per lysimeter. Each lysimeter was fertilized with superphosphate (8.5% P) at a rate equivalent to 30 kg P ha^{-1} while the high-N treatments also received 90 kg N ha^{-1} as NH_4NO_3 incorporated into the top 0.1 m of soil prior to sowing. Subsequent surface applications of urea (30 kg N ha^{-1}) were made on the high N treatment at approximately weekly intervals from 40 days after sowing to give a total application of 300 kg N ha^{-1}. The low-N treatment received only one application of 30 kg N ha^{-1} as urea 76 days after sowing. All lysimeters were watered throughout the growing season to maintain soil matric potential at a depth of 0.15 m in the range -0.01 to -0.06 MPa as measured with a tensiometer. Water applications of less than 35 mm per irrigation (when the soil surface was dry) did not cause soil surface flooding. Waterlogging began 67 days after sowing when free water was kept on the four flooded treatments for 7 days. All surface water was removed from the flooded lysimeters on day 74 using a siphon and subsequent watering was the same as for the control irrigation treatment. To help drain the control irrigation treatments, vacuum suction (0.025 MPa) was applied to the drainage base assembly of the lysimeters on the day of, and for 1 or 2 days immediately following irrigation or rainfall. A total of 101 mm of rain fell during the growing season on 8 days with no daily total exceeding 23 mm.

Below-ground measurements

Soil water content was measured at 0.15 m depth intervals with a calibrated neutron probe (Jayawardane *et al.*, 1984) inserted in a central, vertical access tube in each soil cylinder. Oxygen measurements were made using a Radiometer O_2 sensor[1] type E 5046 on air or water samples withdrawn from horizontally placed samples at 5 depths (0.125, 0.25, 0.55, 0.85, 1.15 m) in the profile. Soil water content, O_2 partial pressure and soil temperature measurements were combined to give estimates of the mass of oxygen per unit volume of soil in each of 5 layers (Meyer *et al.*, 1985) centered on the O_2 measurement depth. These were further combined to estimate the total mass of O_2 per lysimeter.

Root growth and distribution were followed non-destructively using a system (Meyer and Barrs,

[1] Use of trade or firm names is for reader information only and does not constitute endorsement by CSIRO or USDA-ARS of any commercial product or service.

1985) of near-horizontal and horizontal, clear acrylic root observation tubes inserted into the soil core at 0.05–0.25, 0.55, 0.85 and 1.15 m below the soil surface. These tubes were scanned every 7 d with a fibre optic device and roots intercepting lines etched on the tubes were counted.

Above-ground measurements

Growth of main stem leaves were measured on 2 plants per lysimeter from day 41 to day 112 after sowing. Growth was the summation of the daily increase in lamina length from the lamina petiole junction to the leaf tip of all growing leaves on the main stem. Effects of pre-treatment leaf size differences were minimised by calculating relative leaf growth rates (RLGR) (Rawson and Munns, 1984) as

$$\text{RLGR (mm mm}^{-1}\text{ d}^{-1}) = (\log l_2 - \log l_1)/(t_2 - t_1)$$

where l is leaf length (mm) and t is day number. Rates of apparent photosynthesis (APS, mg CO_2 $m^{-2} s^{-1}$) and evapotranspiration (ET, mg H_2O $m^{-2} s^{-1}$) from all plants within each lysimeter were estimated using a portable chamber system (Meyer *et al.*, 1987). Three separate measurements were made over each lysimeter during the midday period from 1100 to 1400 h on day 68 after sowing and on 8 other days up to day 91. These 3 readings were treated as replicate samples for the purpose of analysis. Ambient vapour pressure deficit (VPD, kPa) was calculated from wet and dry bulk temperatures inside the ambient equilibrated chamber prior to each lysimeter measurement. Plant N and P status were assessed by sampling 5 leaves from each lysimeter before (day 67) and after (day 76) the flooding event. Foliage temperature was measured with an Everest Interscience model No. 110^C infrared thermometer which was calibrated against an Everest Interscience model 1000^C calibration source with the emissivity set at 0.98 (Reicosky *et al.*, 1985). Intercepted photosynthetically-active radiation (PAR) was measured during midday using a LiCor line quantum sensor and LI-185A meter^C. Readings from the levelled sensor were taken above the crop canopy and at each of 3 different radial positions below the canopy in each lysimeter. Mean above- and below-canopy values were used to calculate intercepted PAR.

Results and discussion

Soil water and oxygen

Seasonal fluctuations in soil water for the flooded and control irrigated, high-N treatments are shown in Fig. 1. The rain which fell on the second and third days (23 mm in total) of the flooding event kept the lysimeters flooded without additional water; it also caused flooding of the control treatments late on the third day. Water was siphoned from the control treatments on the fourth day and this removal together with the suction applied to the base of the cylinder ensured that soil O_2 levels were not greatly decreased (Fig. 2). Control treatments received 403 mm of irrigation water and 101 mm of rain during the season.

The amount of drainage water which resulted

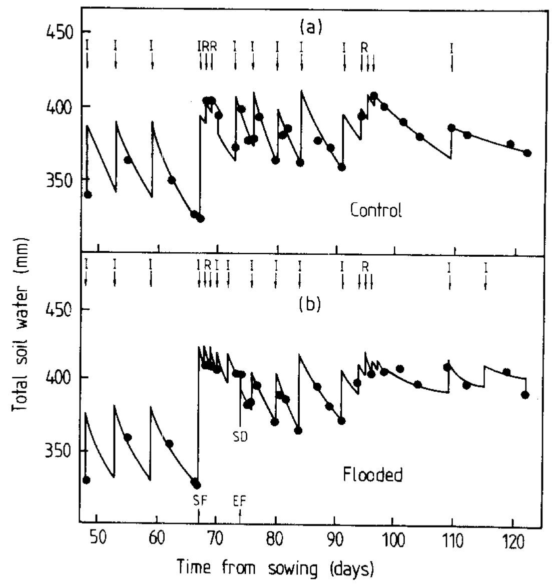

Fig. 1. Total soil water balance for (**a**) control and (**b**) flooded, high nitrogen treatments. **I**, irrigation; **R**, rain; **SD**, surface drainage; **SF**, start of flooding; **EF**, end of flooding. *Solid circles* indicate the mean total soil water content from neutron probe readings with the average standard error of the mean being ± 7.5 mm for the control and ± 12.7 mm for the flooded treatment. The *solid line* is the daily soil water balance interpolated between neutron probe readings, water additions and surface drainage values.

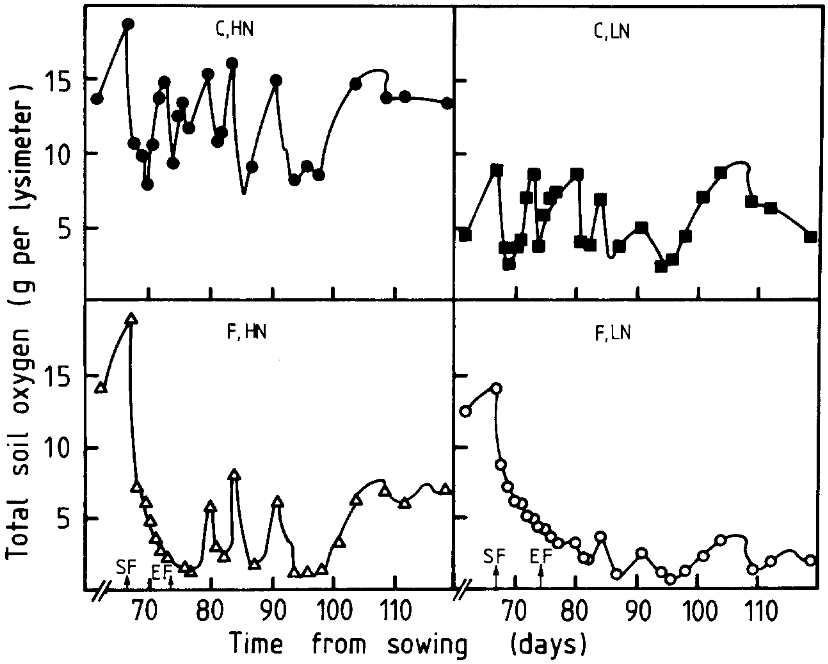

Fig. 2. Total soil oxygen values in the treatments. C, control irrigation; F, flooded; HN, high N; LN, low N. Average standard errors of the mean for each treatment were C, H $\pm$ 1.1 g; F, HN $\pm$ 1.6 g; C, LN $\pm$ 4.4 g; F, LN $\pm$ 0.9 g.

from the suction applied to the base of the 4 control treatments averaged less than 1 mm at each irrigation. This small amount is not shown in Fig. 1 and is a reflection of the very slow internal drainage properties of the Marah clay loam.

The changes in soil O_2 levels through the soil profile as the result of the irrigation treatments were similar to those reported previously and so are not presented here. Response of total soil O_2 to the treatments is shown in Fig. 2. Flooding caused a rapid decrease in total soil O_2 which subsequently stayed at a fairly low level. Difference in response of the N treatments is shown in both irrigation treatments with the high N treatment showing larger fluctuations in O_2 during irrigation cycles and also having mean O_2 levels which were greater. This response was due in part to the greater leaf area and great ET rate (see below) of the high N treatment plants. In addition, the difference in the control irrigation treatments was caused by a consistently greater soil water content (particularly below the 0.5 m depth) in the low-N treatment. This difference (about 20 mm in the 0.6 to 1.1 m depth layer) was present at the start of the experiment and persisted throughout.

Decreased soil O_2 following flooding (Fig. 2) is the result of soil air displacement by water, reduced rates of O_2 diffusion into the profile and use of O_2 by root zone respiration. Nearly all water entry into this soil occurs within the first 2 h of flooding (Mason *et al.*, 1983) so that the volume of air and thus O_2 displaced is accounted for by the change in soil water content during the first day of flooding. After correcting for water displacement of O_2 using the measured change in soil water content during the first day of flooding, the curves of subsequent O_2 depletion by root zone respiration in Fig. 2 were fitted (Fig. 3) to a first order reaction equation (Morris, 1974, p. 248–277). This equation can be integrated to obtain the maximum rate of O_2 consumption at the start of flooding ($\Delta[O_2]_{max}$) and the half life ($t_{1/2}$) of soil O_2. This analysis clearly indicated that the N treatment strongly affected root zone respiration rates. Maximum O_2 consumption rate for the high N treatment was 2.7 times greater than for the low N treatment (Fig. 3). Differences in root zone activity between the treatments is thus indicated.

The values of maximum O_2 consumption rates obtained here (equivalent to 3.5 and 1.3 l m^{-2} d^{-1}

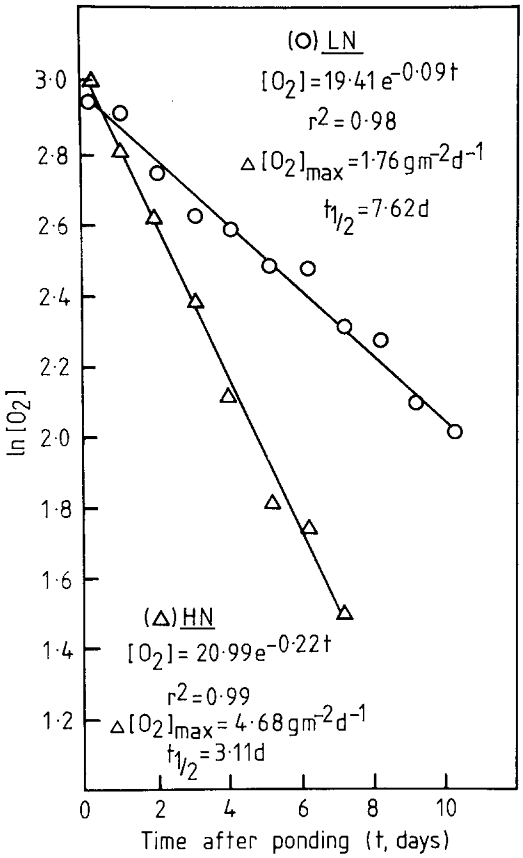

Fig. 3. Change in soil O_2 concentration following flooding in the high N (HN) and low N (LN) treatments. Maximum O_2 consumption rates ($\Delta[O_2]_{max}$) occur at time 0. Half life of O_2 within the system is given as $t_{1/2}$. Mean soil temperature was 24.1 ± 0.1°C.

at 20°C for the high and low-N treatments respectively) are lower than the value (6.71 m^{-2} d^{-1}) measured by Hawkins (1962) from a sandy loam soil with potatoes growing in it. The difference is likely to be due to crop species differences and to soil differences with organic matter content and bulk density favouring greater respiratory activity in the repacked soil used by Hawkins (1962).

Root growth

The seasonal course of total root intercept counts is shown in Fig. 4. At the start of flooding there were 1.8 times as many roots in the high-N treatment as in the low-N treatment. Oxygen consumption differed by a maximum of 2.7 fold between the N treatments indicating that O_2 consumption per unit root length was greater where more N was available for vigorous plant growth. General trends in the root intersection counts indicated that flooding probably caused a reduction in the rate of root growth but this trend did not persist to become statistically significant. There were no major differences in the relative profile distribution of roots between high- and low-N treatments although the high-N plants had a few roots deeper in the profile (> 700 mm depth). Control treatment plants decreased the proportion of their roots in the topsoil layer over time while flooded plants maintained more roots in the upper profile (Table 1). Maintenance of existing roots and sometimes additional growth in the upper soil layers is an adaptation response of cotton (Patrick *et al.*, 1973; Reicosky *et al.*, 1985b) and other species (Belford *et al.*, 1981) to soil waterlogging.

Leaf growth and intercepted PAR

Leaf growth of low-N treatment plants was slower than plants with high-N (Fig. 5). Some reduction in the rate of growth occurred prior to irrigations given on days 53, 59 and 67 after sowing. This reduction (from water deficit stress) was more pronounced in the high-N treatments. Growth rates were steady from the start of flooding (day 67) until about day 80. Significant linear regressions were fitted to each of the treatment growth measurements during this time and slopes of the regressions (high N, C 9.58; high N, F 6.99; low N, C 4.76; low N, F 3.80 mmd^{-1}) were different (P < 0.05) indicating a significant flooding and nitrogen effect. For the period prior to and up to 4 d after flooding. plants which were flooded had higher or the same RLGR as did control treatment plants (Fig. 6). After this time flooded plants had RLGR values equal to or lower than control plants. Thus the effect of flooding on leaf growth took several days to develop.

Measurements of intercepted PAR taken during the flooding event (days 70 and 73) showed a significant difference (P > 0.05) between nitrogen treatments (70.2 and 48.0% for the high and low treatments, respectively), but no difference between flooded and control treatments.

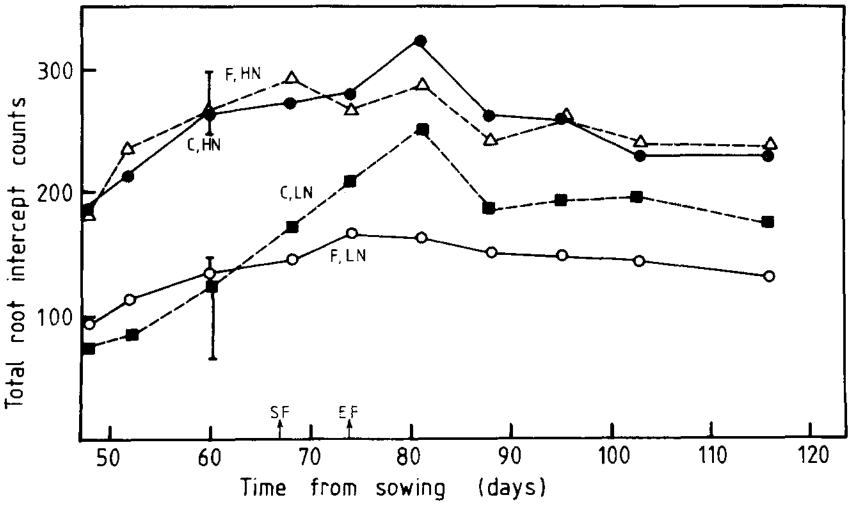

Fig. 4. Total counts of roots intercepting the observation tubes. **SF**, start of flooding; **EF**, end of flooding; **HN**, high N; **LN**, low N; **C**, control irrigation; **F**, flooded. The *bars* on day 60 counts are half the average standard error of the mean for each treatment.

Leaf, foliage and canopy measurements

Results from the statistical analysis of foliage temperature, evapotranspiration and apparent photosynthesis are shown in Table 2. In general there were only a few, non-consistent interaction effects indicated between the N and irrigation treatments.

Low-N-treatment plants had a higher foliage temperature on 3 separate days. A similar effect has been reported for wheat by Seligman *et al.* (1983). Control-irrigation-treatment plants had higher foliage temperatures on days 70 and 72 but on day 73 and afterwards this observation was reversed so that flooded plants showed a higher foliage temperature. This response was similar to that of field-grown cotton reported by Reicosky *et al.* (1985a). These data suggest that the flooded plants were better hydrated for the first 6 d following flooding but subsequently became less so. A similar delayed response to flooding was evident in the data of RLGR.

The effect of the flooding treatment on foliage temperature was not consistently reflected in measurements of ET until day 76, 2 d after the removal of free water from the soil surface. The presence of free water increased measured ET rates by up to 21%; therefore this effect masked any treatment differences. The effect of flooding on decreasing APS, like the increase in foliage temperature and the decrease in RLGR was not evident until 6 d after the start of flooding. On day 69, 2 d after the start of flooding, there was a 9% difference in APS values between the two irrigation treatments. This difference increased to 13% on day 73 when the effect was statistically significant. The difference continued to increase until it reached 39% between days 84 to 112. For the N treatments, there was a fairly consistent difference in APS values of around 39%. This value compares with the 32% difference in intercepted PAR indicating that the efficiency of using intercepted radiant energy for fixing CO_2 also differed between the high- and low-N treatments.

Calculation of a modified transpiration ratio,

Table 1. Relative distribution (%) of root counts through the soil profile during the season for the high N treatments. Flooding occurred between days 67 and 74 after sowing. Any means within the table followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's Multiple Range Test

Depth (mm)	Days after sowing					
	68	88	116	68	88	116
	Control			Flooded		
100	27bc	23c	17d	35ab	33ab	30ab
200	32ab	28ab	26bc	31ab	31ab	33ab
400	34ab	32ab	38a	27bc	27bc	27bc
550	7e	16d	18cd	7e	9de	10d
700	0e	1e	1e	0e	0e	0e

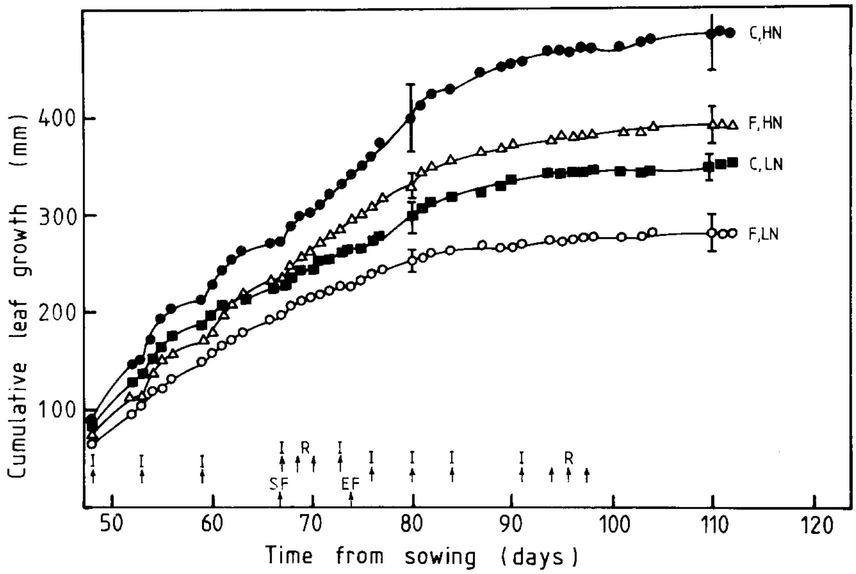

Fig. 5. Mean cumulative leaf growth from day 41 on the main stem of four plants per treatment. **I**, irrigation; **R**, rain; **SF**, start of flooding; **EF**, end of flooding; **HN** high N; **LN**, low N; **C** control irrigation; **F** flooded. *Standard error bars* for each treatment are shown on days 80 and 110.

ET/(APS × VPD) (Bierhuizen and Slatyer, 1965), is an attempt to normalise effects of different canopy leaf areas and different evaporative conditions between days of observation. This ratio indicated that the high-N-treatment plants lost less water per unit of CO_2 fixed than low-N plants and that the flooded plants were less efficient at fixing CO_2 per unit of water loss after day 73 than control irrigated plants. High-N-treatment plants probably had a more efficient photosynthetic mechanism while flooded plants decreased both photosynthetic efficiency and stomatal function. The increase in foliage temperature of the flooded plants on day 73 strongly suggest that stomates began to close, an effect of waterlogging previously observed by Sojka and Stolzy (1980). The normalizing effect of the calculated ratio increased the frequency of significance of the N × irrigation interaction. The interaction was significant on day 73 and on 5 of the subsequent 9 other days of measurement. The direction of the interaction indicated that the low-N, flooded treatment was much more affected by the combined treatment than by the single treatment effects alone. This observation is consistent with the findings of Radin *et al.* (1985), who showed that stomata of low-N cotton plants close more readily in response to water deficit stress than those on plants with adequate N. In our case the low-N plants responded more to the stress imposed by waterlogging, an effect which may have been mediated through stomatal response.

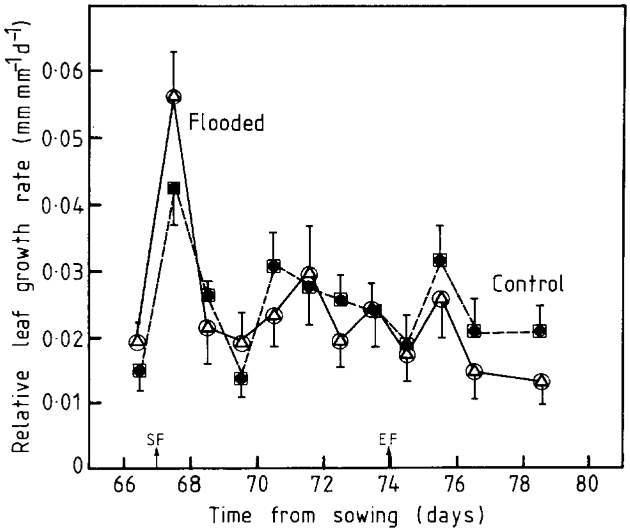

Fig. 6. Change in relative leaf growth rate of all plants in the flooded and control treatments. *Bars* are half the standard error of the mean. **SF**, start of flooding; **EF**, end of flooding.

Table 2. Summary of ANOVA comparisons between treatments (high N *vs* low N; flooded *vs* control irrigation) over time. Flooding occurred between 67 and 74 days after sowing (DAS). **FT**, foliage temperature; **ET**, evapotranspiration; **APS**, apparent photosynthesis; **VPD**, vapour pressure deficit. **H** and **L** indicate whether the high- or low-nitrogen treatment had the larger mean value while **C** and **F** indicate whether the controlled watering or flooded treatments had a larger mean value. Dashes indicate that measurements were not made

Nitrogen treatment					Irrigation treatment			
DAS	FT	ET	APS	ET/(APSXVDP)	FT	ET	APS	ET/(APSXVPD)
67	NS	—	—	—	NS	—	—	—
68	NS	NS	***H	***L	NS	NS	NS	NS
69	NS	NS	***H	***L	NS	***C	NS	NS
70	***L	NS	***H	***L	*C	NS	NS	NS
71	NS	NS	***H	***L	NS	NS	NS	NS
72	NS	—	—	—	*C	—	—	—
73	***L	***H	***H	***L	**F	NS	*C	**F
74	NS	***H	***H	***L	*F	NS	**C	***F
75	***L	***H	***H	***L	**F	NS	NS	NS
76	NS	***H	***H	***l	**F	**C	***C	**F
91	—	***H	***H	***L	—	**C	***C	***F

*, **, *** Indicates significant effect at $P < 0.05$, 0.01 and 0.001 respectively. NS is not significant.

Plant N- and P-status

Change in leaf lamina N- and P-status during the time of flooding are given in Table 3. Petiole samples taken at the same time as the leaf samples showed similar trends. The effect of the high-N treatment in significantly increasing the concentration of total N and decreasing total P in the leaves was clear. During the period of flooding, both N and P levels declined, with the decrease generally being greater in the flooded plants.

Yield

Harvest data are given in Table 4. All measurements showed a significant N effect but the apparent trend for reduced productivity with flooding was not statistically significant. Increased replication would be needed to improve the chance of detecting a significant flooding effect. Apart from this, the present data suggest that a single transient waterlogging does not produce yield depressions comparable to those found when a series of transient events occur (Hodgson, 1982) and therefore, the effects of waterlogging stress may be cumulative.

Conclusion

Rapid reductions in soil O_2 resulted from the displacement of soil air by water and depletion by root-zone respiration. The rate of O_2 consumption was directly related to the size of the root system which, in turn, was strongly influenced by the amount of applied N. Low levels of soil O_2 following flooding did not significantly influence the number of roots observed in the soil profile although flooded plants subsequently developed more roots

Table 3. Total N and P content of leaf lamina samples before (day 67 after sowing) and after (day 76) the flooding event. **HN**, high N; **LN**; low N; **C**, control irrigation; **F**, flooded. Any means within the tables of total N or total P data followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's Multiple Range Test

Day	Total N (g N kg^{-1} dw)				Total P (g P kg^{-1} dw)			
	HN, C	HN, F	LN, C	LN, F	HN, C	HN, F	LN, C	LN, F
67	38.4a	35.1b	22.6e	22.3e	2.7e	2.7e	4.7b	5.9a
76	28.3c	24.3d	19.4f	16.8g	2.1f	1.9f	3.6d	4.1c
Change (%)	−26.3	−30.8	−14.2	−24.7	−22.2	−29.6	−23.4	−30.5

Table 4. Measurements made at harvest (18 Apr. 1983, 122 days after sowing). Values are means of two replicates per treatment. Surface area of each lysimeter was 0.43 m^2. **HN**, high N; **LN**, low N; **C**, control irrigation; **F**, flooded. Means across a row followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's Multiple Range Test

	Treatment			
	HN, C	HN, F	LN, C	LN, F
Mean plant height (mm)	511a	509a	418ab	360b
Boll number	46a	41a	28ab	18b
Plant dry mass (g)	194a	194a	119ab	63b
Boll dry mass (g)	181a	157ab	93bc	48c

in the top 200 mm of soil. The major responses observed during flooding were the rapid decrease in soil O_2 and decreases in plant photosynthetic activity. The causal link between these is unknown but the reduced uptake of N and P during the 7 d flooding period suggested a reduction in root activity, an activity which may be essential for maintaining the integrity of above-ground activity (Trought and Drew, 1981). The data suggest that lowered productivity of the flooded plants occurred through reduced stomatal conductance (inferred from reduced transpiration rates and increased foliage temperatures), reduced photosynthetic efficiency and decreased rates of leaf growth. While the additional N in the high-N treatment appeared to largely negate the long-term effects of flooding (as indicated by the harvest data) the general lack of significant N by irrigation interactions in the short-term measurements suggested that additional supplies of soil applied N failed to prevent the deleterious effects of flooding at or shortly after flooding. It is not clear though whether this was due to the unavailability of N in the soil solution (much could be lost through denitrification) or to the inability of roots to actively take up sufficient N. This question will need to be resolved if agronomic strategies to overcome yield losses due to waterlogging are to be devised.

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